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Anemia tabascana (Anemiaceae), a new species from southeastern Mexico

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Abstract.—We describe ***Anemia tabascana*** (Anemiaceae), a new species from the state of Tabasco in southeastern Mexico. This species is similar to *Anemia phyllitidis* and *Anemia* ×*paraphyllitidis*; however, *A. tabascana* has free veins in the pinnae, and the rachis and distal part of the stipe are glabrescent (vs. at least sparsely pubescent in presumably related species). The closest relative of the new species may be *Anemia nicaraguensis*, which has a similar venation pattern and inclined fertile pinnae but differs in having more rounded or subacute pinna tips, fewer and more equilateral pinnae, and more numerous hairs on the stipes and blades.

RESUMEN.—Se describe ***Anemia tabascana*** (Anemiaceae), una nueva especie del estado de Tabasco en el sureste de México. Esta especie es similar a *Anemia phyllitidis* y *Anemia paraphyllitidis*; sin embargo, *A. tabascana* presenta venas libres en las pinnas, además el raquis y la parte distal del estípite son glabrescentes (frente a al menos escasamente pubescentes en especies presumiblemente relacionadas). El taxon más cercano de la nueva especie puede ser *Anemia nicaraguensis*, que tiene un patrón de venación similar y pinnas fértiles inclinadas, pero difiere en tener los ápices de las pinas más redondeados o subagudos, menos pinnas equiláteras y tricomas más numerosos en los estípites y las hojas.

Key Words.—Conservation; endemic; ferns; humid montane forest; Tabasco.

The genus *Anemia* Sw. was described by Olof Swartz in 1806 and originally placed within the Schizaeaceae; however, in 1841 Johann Heinrich Friedrich Link proposed the family Anemiaceae. Currently, according to modern studies, Schizaeaceae forms a paraphyletic group, so the designation of Anemiaceae as a family with only one genus (*Anemia*) is often preferred (Labiak, Mickel, and Hanks, 2015; Smith *et al.*, 2006; PPG I, 2016). Anemiaceae comprises about 115 species worldwide and is distributed mainly in North

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America, South America, Africa, and India (Mickel, 2016; Mickel and Smith, 2004; PPG I, 2016). Latin America has the highest species diversity of the genus. Within the Neotropics, Brazil, especially the Planalto region, is most species-rich with ca. 70 species, followed by Mexico with 21 (Lage, Schwartsburd, and Alves-Araújo, 2017; Mickel, 2016; Mickel and Smith, 2004). In Mexico, the genus is distributed throughout the country; however, most species are found in regions along the Pacific coast. Most of the Mexican species are considered by Mickel (2016) to belong to subg. *Anemia*, and our new one is among these; a few belong to subg. *Anemiorrhiza*, characterized by long-creeping rhizomes, distichous fronds, and spiculate spore ridges (vs. compact to short creeping rhizomes, polystichous fronds, and non-spiculate ridges in subg. *Anemia*). Four species (not all exclusively Mexican in their ranges) occur in states with tropical vegetation in southeastern Mexico, in addition to several species that are widely distributed throughout the country (Mickel, 2016; Mickel and Smith, 2004); these more restricted species are *Anemia cicutaria* Poepp. ex Spreng., *A. familiaris* Mickel, *A. muenchii* Christ, and *A. speciosa* C.Presl.

Anemia has short-creeping or ascending rhizomes. The fronds are generally erect but rarely form rosettes, are 1–3-pinnate, and are herbaceous or leathery. The veins in the pinnae can be free or reticulate. Most species are hemidimorphic, with fertile basal pinnae different in form from the sterile ones and usually erect (rarely horizontal) (Mickel, 1982, 2016).

Although Mexico has one of the best-documented fern floras in the tropics and subtropics (Mickel and Smith, 2004), floristic inventories in remote and botanically largely unexplored areas are needed, because there are still many undiscovered species that may be endangered by ongoing deforestation and habitat loss. For example, in the last four years in Veracruz, 32 new records have been documented for the state; these findings are the result of field research and study of collections in herbaria (Carvajal-Hernández *et al.*, 2018a; Krömer *et al.*, 2015). In the neighboring state of Tabasco, the pteridophyte flora has been recently increased by 51 species (Carvajal-Hernández *et al.*, 2018b; Cetzal-Ix, 2013 a, b), in addition to the new one presented here. These findings demonstrate the importance of further floristic studies, and the task of training of specialists in different taxonomic groups is urgent in continuing to document biodiversity (Mora *et al.*, 2011).

The material used for the description of the species new to science was recollected in the town Cerro Las Flores, Municipio of Huimanguillo, Tabasco, in southeastern Mexico, in a tropical rain forest and in the transition zone between tropical rain forest and humid montane forest.

Anemia tabascana Carv.-Hern., E. E. Cord. & T. Krömer, **sp. nov.** (Figs. 1, 2)

Type: MEXICO. Tabasco: Mpio. Huimanguillo. Cerro La Antena, perteneciente al ejido Villa de Guadalupe, subiendo por la brecha de la iglesia, pasando el pastizal, 400 m snm 17° 21′ 0.634″ N 93° 36′ 0.834″ W, 2 Nov 2015, *E. E. Córdova-Hernández and C. M. Burelo-Ramos 55* (Holotype: UJAT; Isotypes: CICY, MEXU, UJAT, XAL).

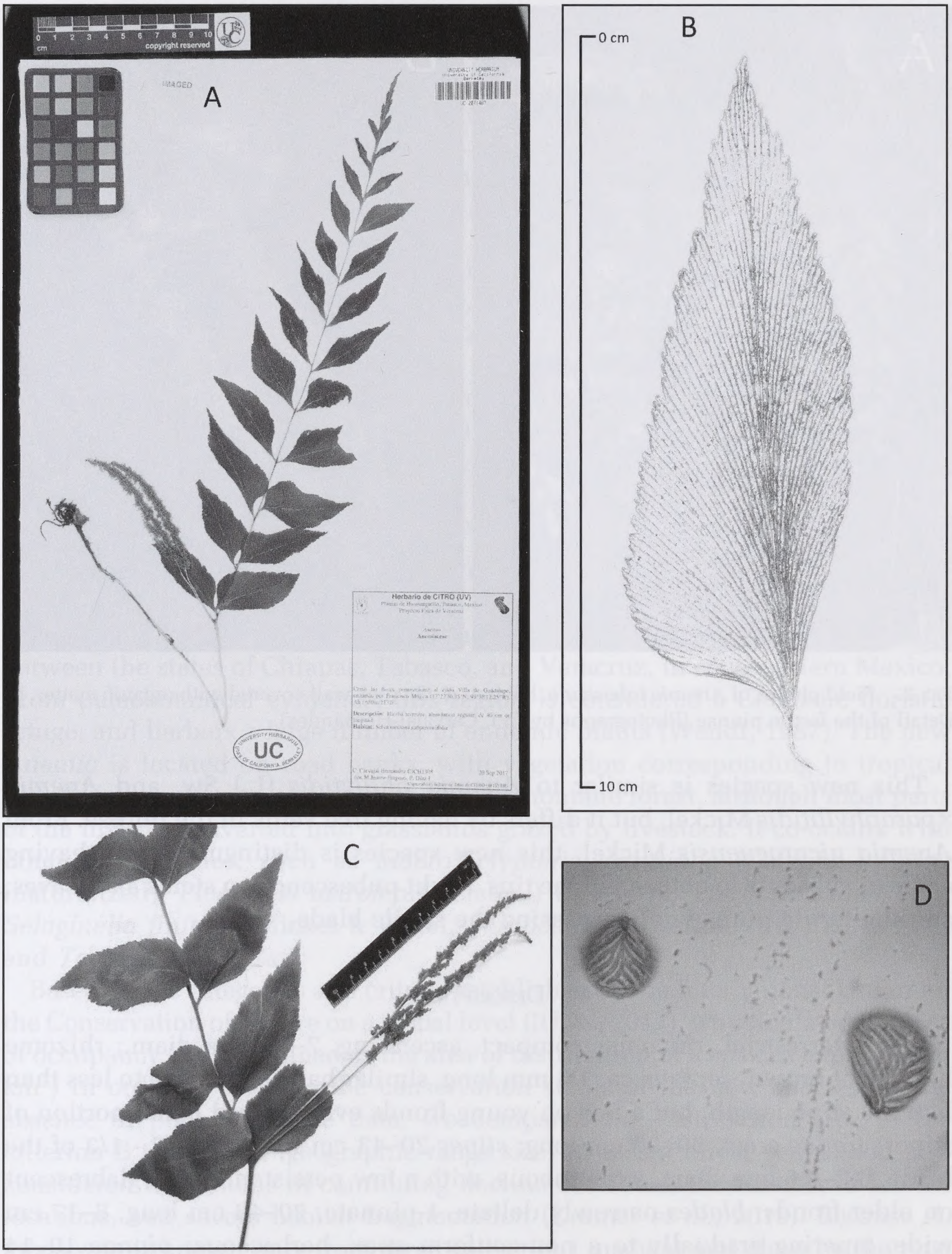

FIG. 1. *Anemia tabascana.* A. Full specimen; B. Pinna detail highlighting free veins; C. Proximal pinnae (Paratype MEXU); D. Spores. The images correspond to the paratype (*C.I. Carvajal-Hernández et al., 1308*) (Photographs A, B, C by C. I. Carvajal-Hernández and D by Roberto Castro-Cortés).

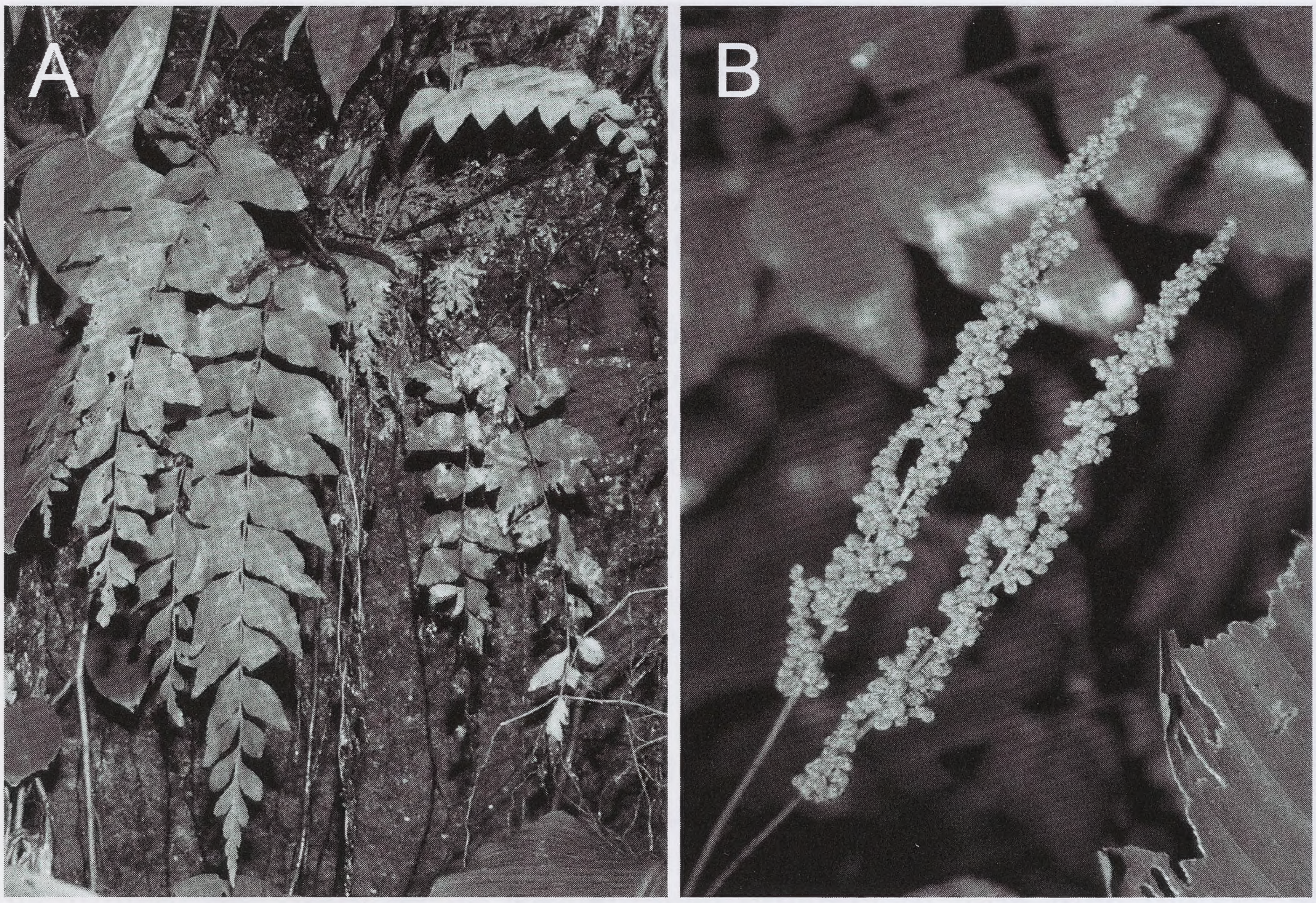

FIG. 2. Field photos of *Anemia tabascana*, habitat. A. On rock wall covered with organic matter. B. Detail of the fertile pinnae (Photographs by C. I. Carvajal-Hernández).

This new species is similar to *Anemia phillytidis* (L.) Sw. and *Anemia ×paraphyllitidis* Mickel, but it differs by having free veins in the pinnae. From *Anemia nicaraguensis* Mickel, this new species is distinguished by having acute or subacute to obtuse pinnae tips, slight pubescence on stems and leaves, and the fertile pinnae not surpassing the sterile blade.

DESCRIPTION

Plants terrestrial, *rhizomes* compact, ascending, 7–11 mm diam.; rhizome hairs light brown, septate, ca. 1.3 mm long, similar hairs extending to less than half the stipe length, but a few on young fronds even toward distal portion of stipes; *fronds* erect, 50–90 cm long; *stipes* 20–43 cm long, ca. 1/2 - 1/3 of the blade, 0.2–0.6 mm diam, stramineous, with a few persistent hairs, glabrescent on older fronds; *blades* narrowly deltate, 1-pinnate, 20–48 cm long, 8–17 cm wide, tapering gradually to a non-conform apex, herbaceous; *pinnae* 10–14 pairs, 5–10 cm long, 1.5–3 cm wide, opposite to subopposite, each with a distinct costa, the proximal ones strongly inequilateral, excavate basiscopically, lanceolate to ovate, cuneate at basiscopic margin, rounded on acroscopic margin, short-stipitate 1–3.5 mm, apices acute to obtuse, margins crenate to denticulate; veins all free, 2–3 times forked, prominulous adaxially; blade surfaces abaxially glabrous, with a few, minute light brown septate hairs grouped along the axes and extending onto main pinna veins adaxially, these becoming shorter, falcate, more hyaline, and fewer toward the pinna margins on a few veins, even with a few falcate hairs to ca. 0.5 mm long midway between adjacent veins, glabrescent; fertile pinnae approximate to lowermost sterile pinnae, erect, arising at angles of 75° to 90° with respect to the rachis, petiolulate ca. 3–9 cm, 11–21 cm long, ca. 1/3–1/2 to surpassing the sterile blades in length; spores striate, ridges smooth, closely spaced, without bacula.

PARATYPES: MEXICO. Tabasco: Mpio. Huimanguillo, Cerro Las Flores, perteneciente al ejido Villa de Guadalupe, entrando por Francisco Mújica, 650 m, 17° 22′ 36.7″ N, 93° 38′ 12.25″ W, 20 Sep 2017, *C. I. Carvajal-Hernández et al. 1308* (CIB, MEXU, UAMIZ, UC, XAL); Cerro La Antena, perteneciente al ejido Villa de Guadalupe, entrando por la iglesia del ejido, pasando el pastizal, 400 m, 17° 21′ 0.634″ N 93° 36′ 0.834″, 25 Apr 2018, *M. Campos-Díaz et al.* 76 (MEXU, UJAT).

DISTRIBUTION AND HABITAT

Anemia tabascana is so far known only from the type locality at cerro Las Flores also known locally as Cerro La Antena. There are collections of the species made on different slopes of the same hill, in the tropical border zone between the states of Chiapas, Tabasco, and Veracruz, in southeastern Mexico. From paleobotanical evidence, this region is considered a Cenozoic floristic refuge, and harbors a large number of endemic plants (Wendt, 1987). The new *Anemia* is located on road banks, with vegetation corresponding to tropical rain forest near the transition with humid montane forest, although most parts of the hill are converted into grasslands grazed by livestock. It co-occurs with other fern species, such as *Macrothelypteris torresiana* (Gaudich.) Ching (naturalized), *Pleopeltis astrolepis* (Liebm.) E. Fourn., *Pteris altissima* Poir, *Selaginella finitima* Mickel & Beitel, *Serpocaulon triseriale* (Sw.) A. R. Sm., and *Tectaria incisa* Cav.

Based on the categories and criteria established by the International Union for the Conservation of Nature on a global level (IUCN, 2017), we calculated the area of occupancy (AOO; defined as the area of distribution of a species expressed in km^2) in order to evaluate the conservation status of the new species. In the absence of population-size data, we compared the distribution area to the criterion B thresholds (geographic range size) to assign threat status, and also considered indications of continuing decline of habitat, the number of known locations, and severe habitat fragmentation (Krömer *et al.*, 2019). Because *A. tabascana* is known only from three collections made at and close by the type locality (AOO: 4 km^2), where its habitat is heavily threatened by deforestation and changes in land use, it corresponds to the category of Critically Endangered (CR) B2ab(ii,iii) according to the IUCN (2017); however, more botanical exploration in the region is needed to detect possible new populations.

The critical conservation situation of this species, added to the biogeographical importance of the area as a floristic refuge, makes it desirable to conduct taxonomic, biogeographic, and ecological studies that support future conservation strategies.

ETYMOLOGY

The specific epithet refers to the state of Mexico where the species was collected.

NOTES

The form of the fronds and blades of *A. tabascana* is reminiscent of *A. phyllitidis* (Argentina, Brazil, Bolivia, Caribbean, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, and Venezuela) and *A.* ×*paraphyllitidis* (Caribbean, Costa Rica, El Salvador, Mexico, and Venezuela), which is the putative hybrid between *A. phyllitidis* and *A. semihirsuta* Mickel. All of these taxa have unlobed pinnae. However, both *A. phyllitidis* and *A.* ×*paraphyllitidis* have a conspicuous indument along the rachises and stipes, in addition to anastomosing (reticulate) blade venation (Table 1). This is contrary to *A. tabascana*, which has free venation and rachises and stipes with slight pubescence, concentrated at the junctions between pinnae and the rachis and the proximal part of the stipe. In the sum of its characters, *A. tabascana* may be most closely related to *A. nicaraguensis* (Mickel, 2016), which is known from only four collections from Nicaragua and three from Belize (Mickel, 2016). *Anemia tabascana* will key approximately to *A. nicaraguensis* in Mickel (2016), but the latter has 3–7 pairs of sterile pinnae, more rounded or subacute pinna tips, more equilateral proximal pinnae, and more numerous hairs on the stipes, rachises, and blades. *Anemia nicaraguensis* agrees with *A. tabascana* in having the fertile pinnae inclined away from the rachis at an angle (Mickel, 2016) and prominulous veins adaxially. Mickel (2016) compared *A. nicaraguensis* to both *A. muenchii* and to *A.* × *paraphyllitidis* (= *A. phyllitidis* × *semihirsuta*, having malformed spores), differing from both in having free veins. Spores of *A. tabascana* appear

TABLE 1. Comparison of characters of *Anemia tabascana* with morphologically related species of the genus *Anemia*.

	A. tabascana	***A. nicaraguensis***	***A. phyllitidis***	***A.* × *paraphyllitidis***
Indument in rachis and stipe	Slightly pubescence	Conspicuous	Conspicuous	Conspicuous
Pairs of pinnae	10-14	3-7	2-5	5-9
Pinnae tip	Acute to obtuse	Rounded or subacute	Acute	Acute to obtuse
Veins	Free	Free	Reticulate	Reticulate
Fertile pinnae	No surpassing the sterile blade	Somewhat surpassing sterile blade	Surpassing the sterile blade	Equal or surpassing the sterile blade
Spore	Without bacula	With bacula	With spine	Abortive

well formed and are different from those of *A. nicaraguensis* since they have ridges without bacula (Fig. 1 D), contrary to the baculate crests of *A. nicaraguensis* (Mickel, 2016). In addition, *A. tabascana* has short fertile pinnae, generally less than half the blade length, and these arise at angles of 75° to 90° with respect to the rachis, compared to other Mexican *Anemia* species where the fertile pinnae surpass the blade length and are at smaller angles with respect to the rachis.

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Spore dispersal of *Selaginella denticulata*, *S. helvetica,* and *S. selaginoides*, and the significance of heterospory in Selaginellacae

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Abstract.—Little is known about the functional significance of heterospory in land plants, nor about how species ensure that mega- and microspores, which have strongly different wind dispersal, are dispersed over similar distances to ensure cross-fertilization. We studied active ejection distances and heights of megaspores of *Selaginella denticulata*, *S. helvetica*, and *S. selaginoides*. Under laboratory conditions, the maximum horizontal and vertical ejection distances of megaspores from the sporangia were 24 cm and 22 cm for *S. denticulata*, 65 cm and 45 cm for *S. helvetica*, and 120 cm and 76 cm for *S. selaginoides*. The function of this active spore ejection thus should not only be seen in the ability of horizontal dispersal but also as a means to bring the megaspores into the wind currents. Under laboratory conditions, microspores of all three species showed a maximum horizontal ejection distance of about 10 cm. However, experiments in the open showed that under natural conditions with wind, microspore dispersal occurs over much longer distances and that the megaspores are partly also wind assisted and reach similar distances. In addition, we observed synaptospory, in which microspores electrostatically adhered to megaspores and were dispersed with them. Our results suggest that the active ejection of the megaspores is a means of ensuring similar dispersal distances of micro- and megaspores and thus cross-fertilization. Very little is known about the breeding system in *Selaginella*, but we surmise that both self-fertilization and outcrossing occur.

Key Words.—Ejection distances, field experiments, lab experiments, megaspores, microspores, *Selaginella* life cycle, spore size

Heterospory, in which many small male spores and a reduced number of large female spores are produced, is an evolutionary innovation that occurred repeatedly in the history of land plants. Despite the importance of heterospory as a precursor to the evolution of seeds, the functional significance of heterospory has not yet been fully explained. Petersen and Burd (2017, 2018b) suggested that heterospory may have evolved when the increasingly tall and complex Devonian vegetative communities presented competitive conditions that made large spore size advantageous. Alternatively, heterospory may be a kind of reinvention of anisogamy within the context of a sporophyte-dominant land plant life cycle (Petersen and Burd, 2017). These ideas are consistent with current knowledge, but remain to be more fully tested.

While the advantages of heterospory remain poorly understood, the development of mega-and microspores leads to an obvious challenge, which is to guarantee that after dispersal the two spore types are in close enough proximity to allow successful fertilization. Studying the surface ornamentation of micro- and megaspores, Wang, Zhang, and Liu (2018) recently showed that synaptospory (Kramer 1977), *i.e.*, the joint dispersal of adhered spores, may play a role in avoiding this challenge.

The large genus *Selaginella* (ca. 800 species) in the lycophyte lineage is characterized by growing in a wide range of habitats (with emphasis to tropical areas), showing highly diverse growth forms (Zhou and Zhang 2015), and by having heterospory. Interestingly, the degree of heterospory differs between different groups of *Selaginella*, such as those with articulate and non-articulate stems. When referring to published results, the articulate forms have microspores of 0.019-0.079 mm and megaspores of 0.202-0.473 mm in diameter, whereas the non-articulate species have similarly sized microspores (0.025-0.032 mm) but much larger megaspores (0.245-1.300 mm) (Fraile, Somers, and Moran, 1995; Hellwig, 1969; Korall and Taylor, 2006; Zhou *et al.*, 2015). This variation suggests that spore size within *Selaginella* shows a phylogenetic signal that may also related to environmental conditions. Up to date, nearly nothing is known about the *Selaginella* mating system. *Selaginella apoda* has been found to be fully self-compatible (Schulz *et al.*, 2010), whereas VanBuren *et al.* (2018) investigating *S. lepidophylla* documented that heterozygosity (presumably as a result of outbreeding) is important in the context of its desiccation-tolerance.

Two different types of active spore discharge occur in *Selaginella* (Webster 1995). It was Goebel (1901) who showed that the megasporangium ejects the megaspores in a manner quite different from the microspore release mechanism of the microsporangia. He gave a detailed description of the mechanism of megaspore release that was recently rediscovered by Page (1989), who described the active megaspore discharge mechanism as "compression and slingshot ejection" caused by a special differentiation of the sporangium wall, compared to the more passive release by the microsporangia. The numerous small microspores (the three species studied by us have a microspore diameter of about 0.03-0.06 mm) formed by the microsporangia (Koller and Scheckler, 1986) are in most cases dispersed by active ejection during dehiscence, as are the four large megaspores (diameter about 0.25-0.60 mm) produced by the macrosporangia (Korall and Taylor, 2006). The microspores of *Selaginella* are similar in size to the wind-dispersed spores of mosses and of pollen of seed plants, so that we can expect comparable passive dispersal patterns (Miles and Longton, 1992; Ghazoul, 2005; Friedman and Barrett, 2006). In contrast, the sling shot mechanism of megaspores leads to active dispersal and seems to be only partially influenced by wind.

The differences of spore release are therefore related to the subsequent wind-dispersal of the spores and the active sling shot mechanism of megaspores. The question thus emerges, whether the more active ejection of the megaspores is a means for compensating for less efficient wind dispersal, thus ensuring that micro- and megaspores are deposited close enough for fertilization to occur. In earlier publications, Filippini-De Giorgi, Holderegger, and Schneller (1997) and Schneller, Gerber, and Zuppinger (2008) studied the extent of active horizontal micro- and megaspore dispersal of different *Selaginella* species. In the present study, we conducted similar experiments with the circum-mediterranean *S. denticulata* (L.) Spring, European and northern Asian *S. helvetica* (L.) Spring and the circum-temperate *S. selaginoides* (L.) Beauv. ex Schrank & Mart. In addition, we executed experiments to measure the height to which megaspores are ejected. To simulate more natural conditions, Fillippini-De Giorgi, Holderegger, and Schneller (1997) used artificial wind produced by a small electric propeller. To obtain an even a more realistic view of spore dispersal under natural conditions, we arranged experiments in the open.

Material and Methods

Fertile plants of *Selaginella selaginoides* were collected in the upper region of Selva Secca near Acquacalda (Canton Ticino, Switzerland N 46.538028, E 8.832319, 1810 m, in the valley of Piora (Canton Ticino N 46.551416, E 8.718260, 1950 m) and in the region of Kunkelspass near Tamins (Canton Grisons, Switzerland, N 46.855024, E 9.405233, 1360 m). All of them were growing in open or partly shadowed grassy meadows. Fertile plants of *Selaginella helvetica* were collected in the region of Vasorta near Tamins (N 46.823712, E 9.393051, 610 m) and in the region of Kunkelspass (coordinates see above). Fertile plants of *Selaginella denticulata* were collected in the Imbros Gorge, Crete (N 35.241022, E 24.166833, ca. 450 m). All collected plants were kept moist in plastic bags and used for the experiments within three days after collection.

In the laboratory, we conducted different experiments. The stobili of the study species usually bear basal megasporangia and apical microsporangia. For all the experiments, we attached the shoots to the lateral sides of small plastic boxes (2 cm in height), with the fertile parts left unattached for about 1-3 cm above the fixed part. The distance of the spikes to the floor corresponded approximately to natural conditions, ranging from 2 cm to 8 cm. To measure the distance of spore ejection from the starting point, we used glass panels covered with a thin layer of petroleum jelly to trap the dispersed spores. The selection of the glass panels with petroleum jelly allowed recognizing the white megaspores of all three species, the light-yellow microspores of *S. helvetica*, and *S. denticulata* and the orange-brown tetrads of microspores of S. *selaginoides* (shown in Fig. 1 in black and white).

To study the height at different distances from the source at which spores are ejected, we used glass plates of 40 cm x 80 cm covered with a thin layer of petroleum jelly that were set upright and parallel to the fertile shoots at distances of 3 cm, 30 cm, and 40 cm of the individual *Selaginella* species. All the experiments were conducted in the laboratory at 22°C and approximately 60% relative humidity and lasted approximately 20 hours. The significance of the different measurements was calculated using a Kruskal-Wallis Test (Sokal and Rohlf, 1995).

We carried out a third set of experiments using *S. helvetica* in the open in a stone-flagged place under the influence of natural wind. An anemometer

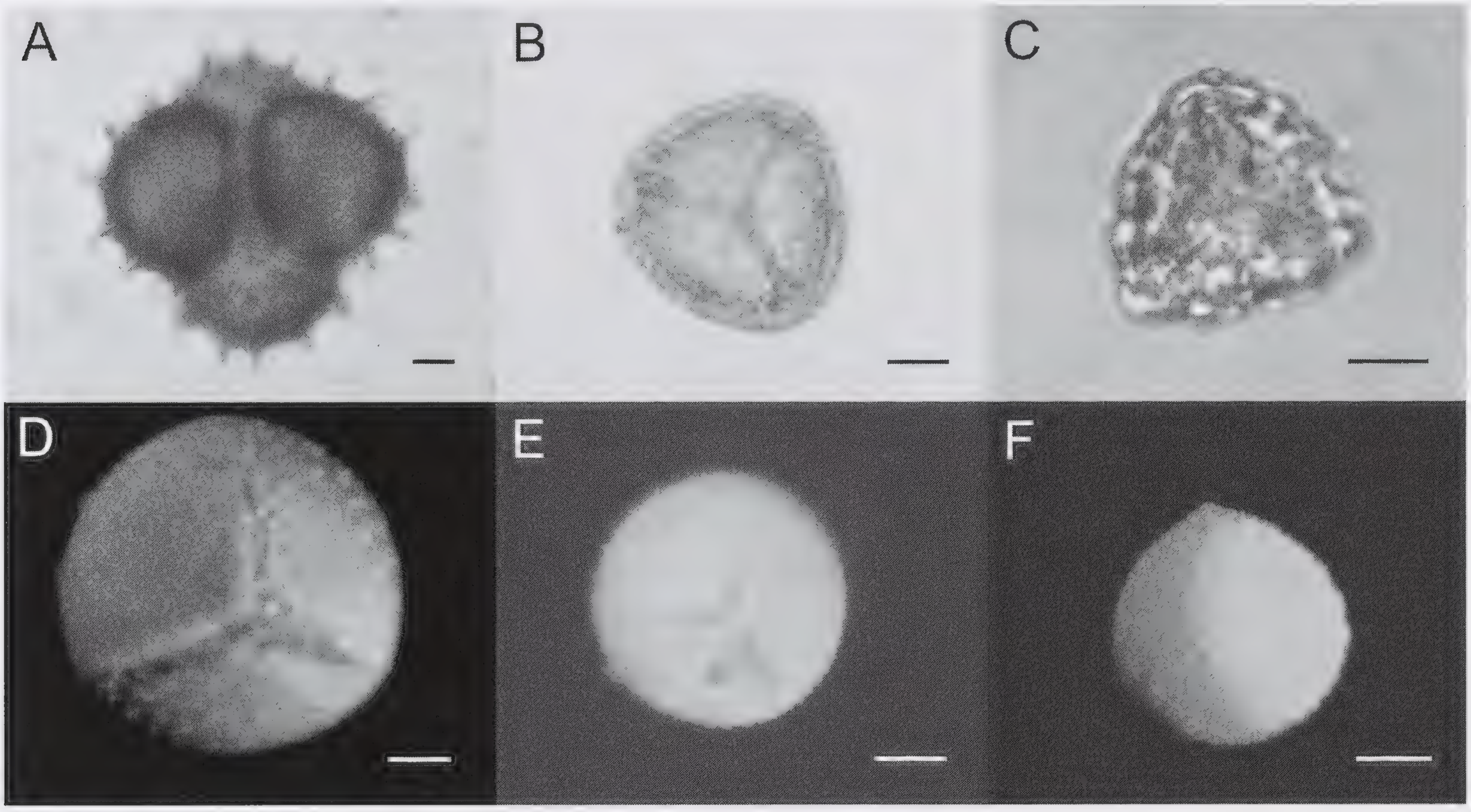

FIG. 1. Microspores (upper row) and megaspores (lower row) of *Selaginella selaginoides* (A: tetrade, D), *S. helvetica* (B, E), and *S. denticulata* (C, F). Scale bars in A-C 1 μm, in D-F 100 μm.

(Windware wind data logging kit) was positioned right beside the experimental arrangement of spikes to measure the wind speed, which varied between 0 m/sec and 5 m/sec. The size of the observed area was 7 m x 1 m. We conducted two experimental runs, each lasting 12 hours on dry sunny days without rain.

RESULTS

The median dispersal distances of actively spread megaspores of *Selaginella denticulata*, *S. helvetica*, and *S. selaginoides* in the lab were highly significantly different between species (Kruskal-Wallis test, df=2, K=1813.09, $P<0.001$). Megaspores of *S. selaginoides* had the highest median (60 cm) and maximum (120 cm) dispersal distances, followed by *S. helvetica* (40 cm and 65 cm), *S. denticulata* (15 cm and 24 cm), and microspores of all three species (10 cm and 15 cm) (Fig. 2). Differences were also mirrored in the experiment focusing on ejection height. At a distance of 3 cm, the difference of the median between species was significant (Kruskal-Wallis test df=2, K=55, $P= 0.05$) (Fig. 3). The highest ejection found in *S. selaginoides* at 3 cm was 85 cm (median 45 cm), 35 cm (median 20 cm) in *S. helvetica*, and 15 cm (median 10) in *S. denticulata*. There was no significant difference regarding the distances of 30 cm and 40 cm (Fig. 3) Megaspores of *S. selaginoides* and *S. helvetica* showed a similar maximal height of 28 cm at 30 cm distance (median 14 cm) and 19 cm at 40 cm distance (median 6 cm).

The investigations done outdoors using *S. helvetica* showed that wind led to a very different pattern of actual spore dispersal. Under conditions with wind speeds of up to 5 m/sec, despite the different active ejection distances found in the lab experiment, micro- and megaspores were spread over similar distances

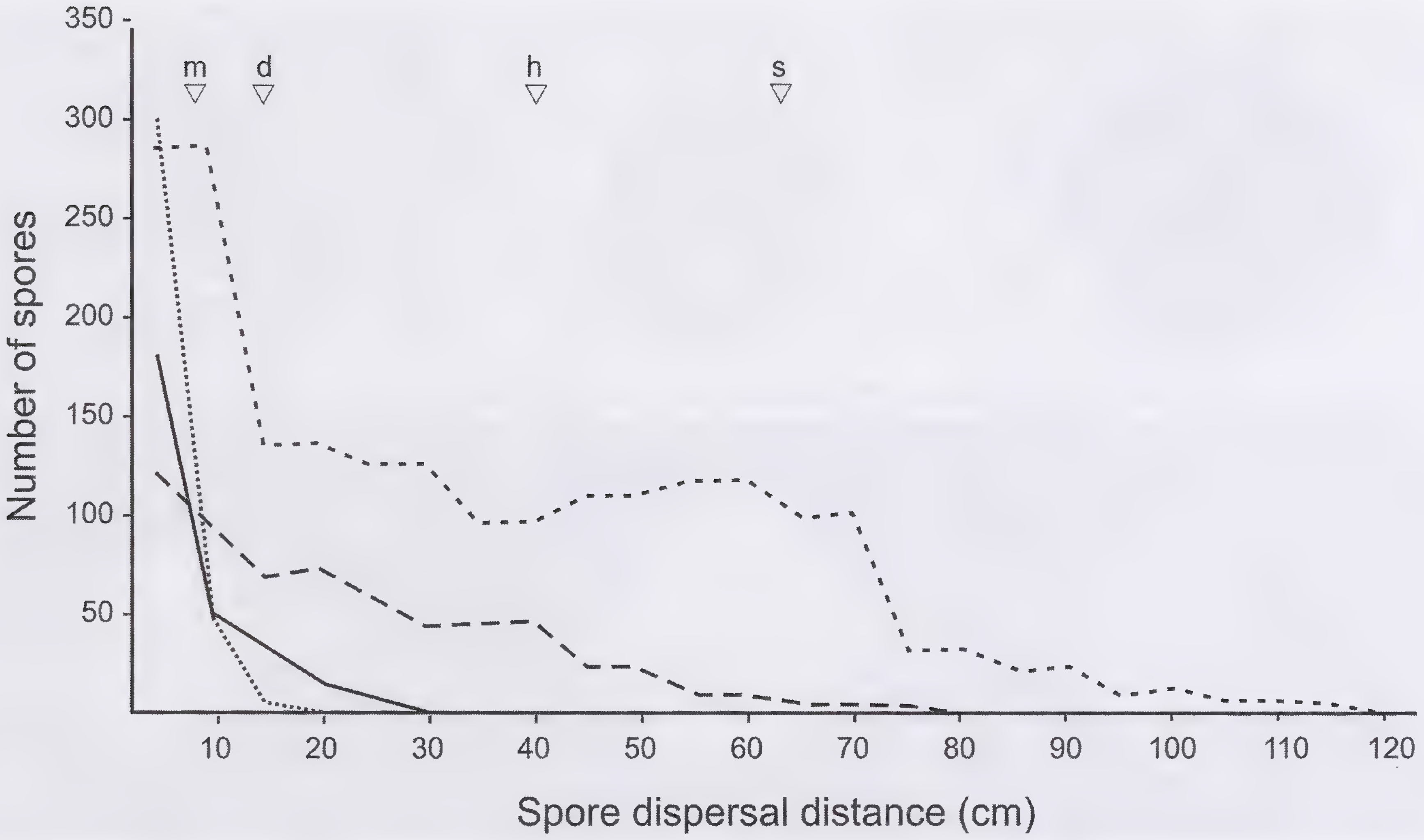

FIG. 2. Ejection distances of megaspores of *Selaginella denticulata* (continuous line), *S. helvetica* (short-dashed), and *S. selaginoides* (long-dashed) and of microspores (dotted) of all three species under laboratory conditions. Arrows on top denote median ejection distances for microspores (m), *S. denticulata* (d), *S. helvetica* (h), and *S. selaginoides* (s).

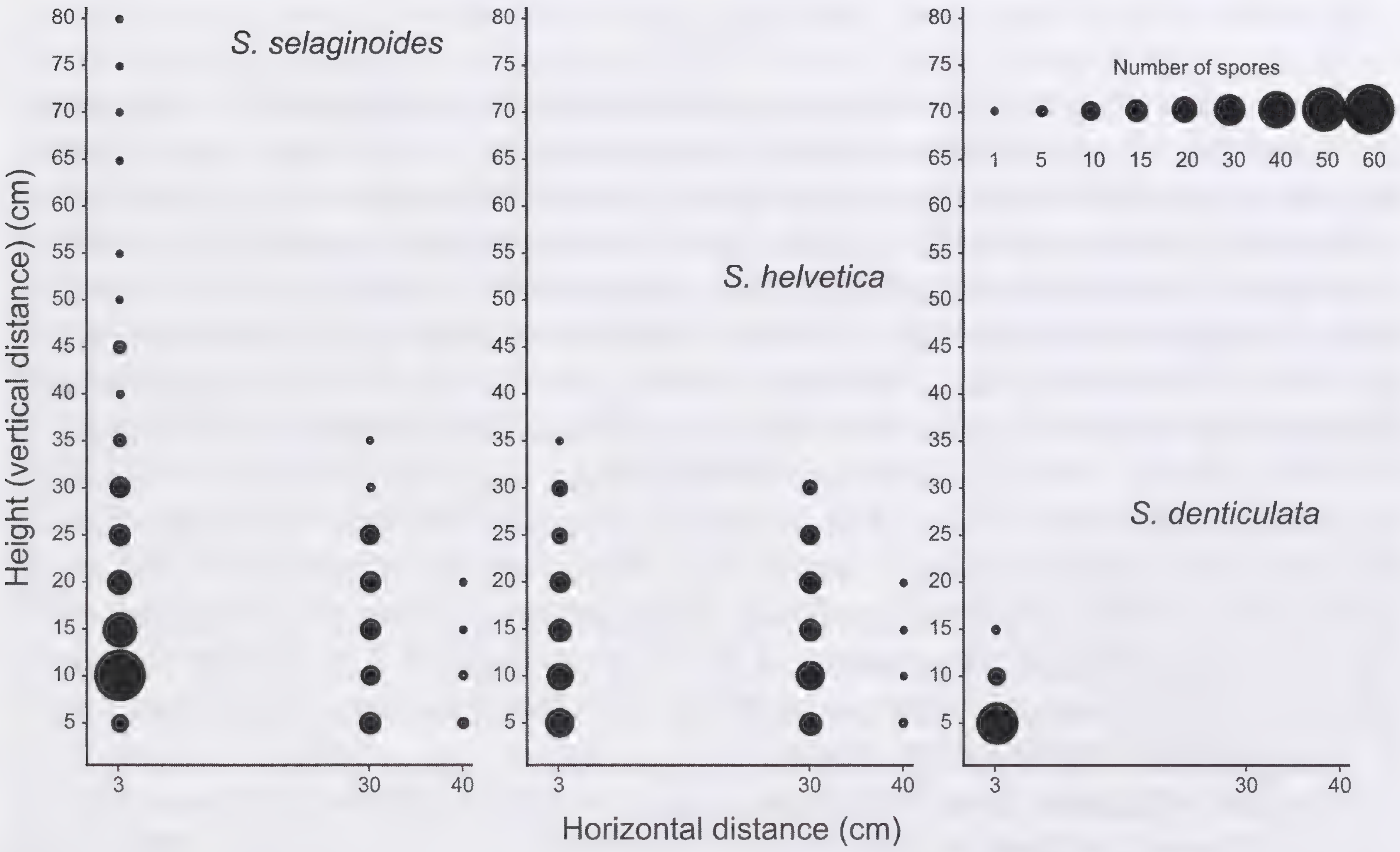

FIG. 3. Numbers of megaspores ejected to different 5 cm height classes by three species of *Selaginella* at three distances from the source plants (3, 30, 40 cm) under laboratory conditions.

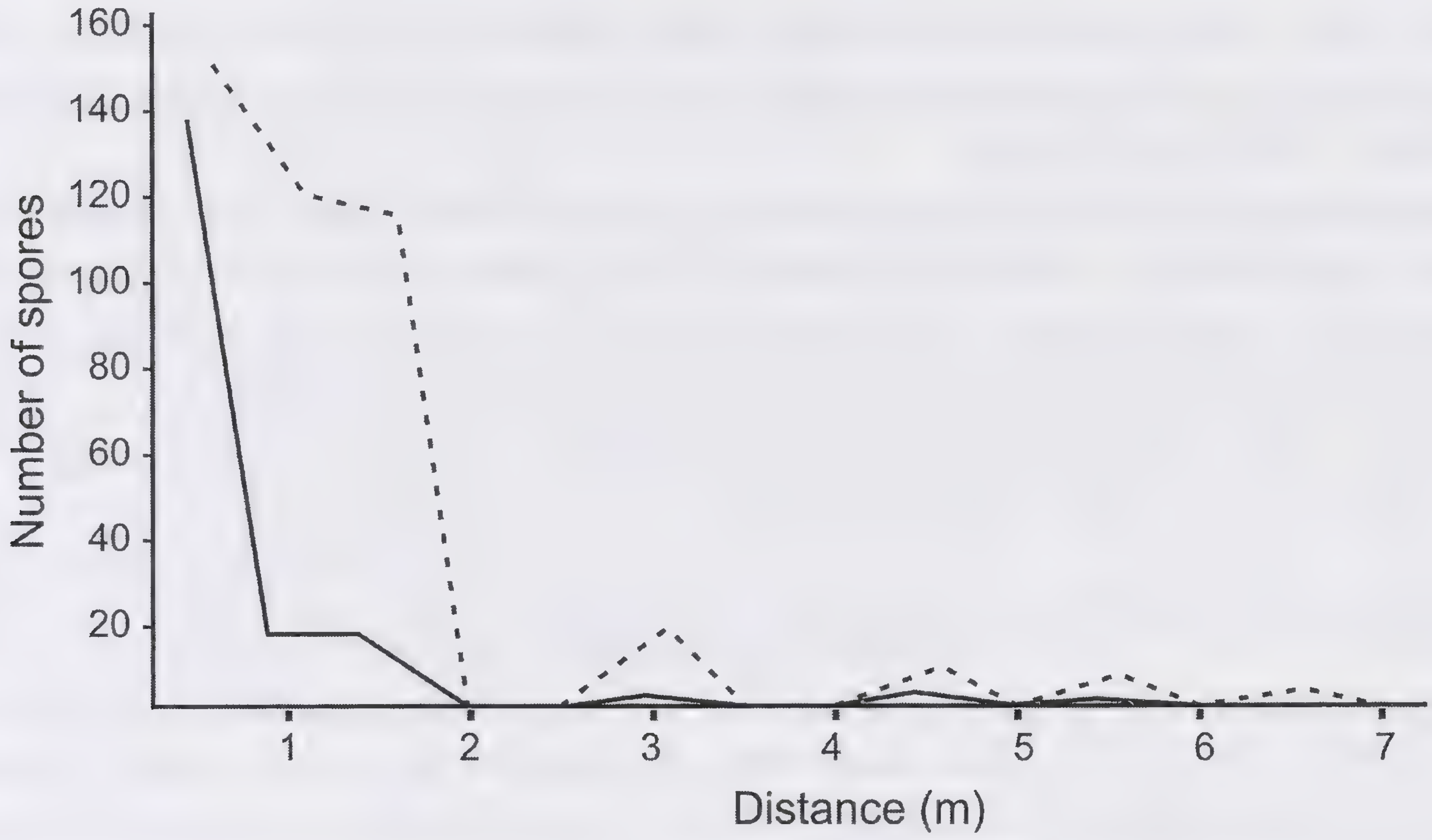

FIG. 4. Dispersal frequencies of mega- (continuous line) and microspores (dashed line) of *S. helvetica* under field conditions.

(Fig. 4). We further observed that megaspores are electrostatic and that microspores adhered to their surfaces (Fig 5).

DISCUSSION

We found that the distances over which megaspores are dispersed under laboratory conditions by the slingshot mechanism varied significantly when comparing different species of *Selaginella*, with median distances ranging of 15-60 cm and maximum distances of 24-120 cm. This compares well with the results of Filippini-De Giorgi, Holderegger, and Schneller (1997), who measured maximum distances of 60 cm in *S. martensi*, *S. anceps*, and *S. pallescens*, and 15 cm in *S. lepidophylla* and *S. kraussiana*. In addition to

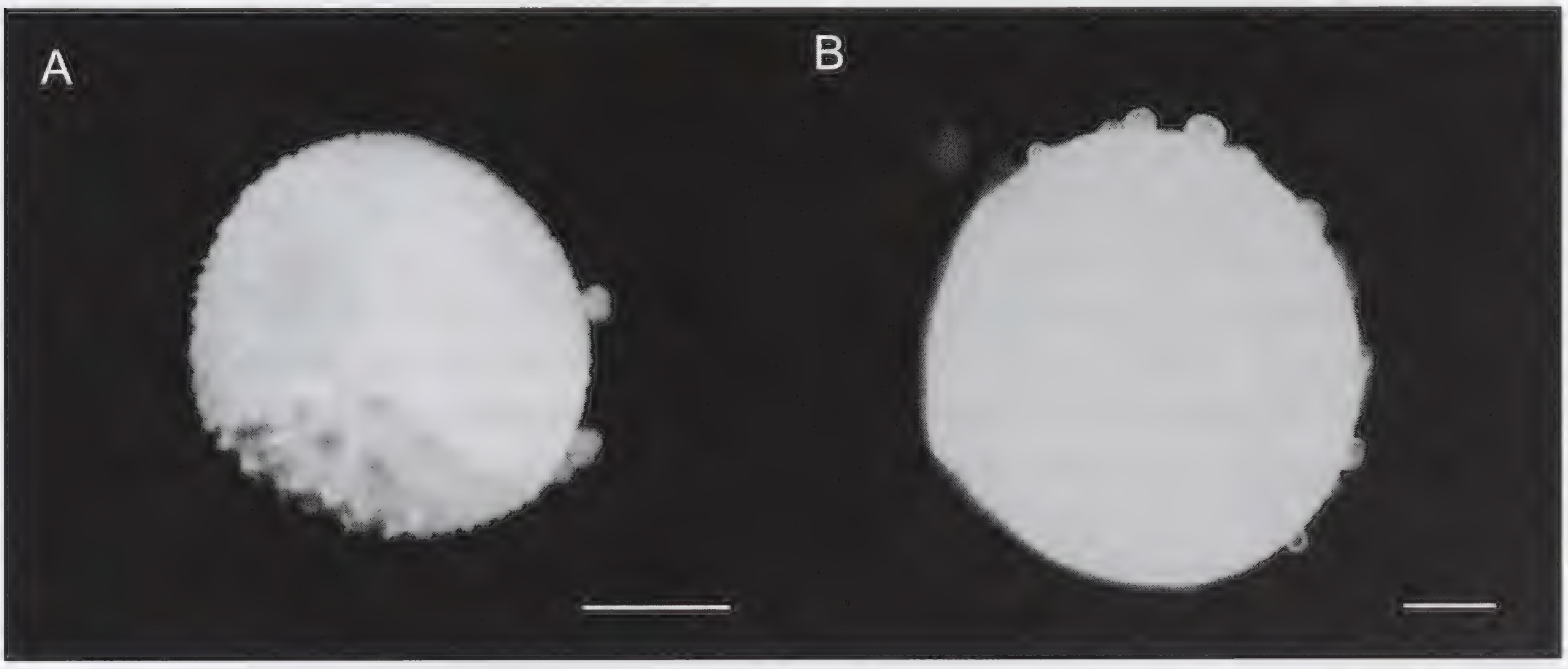

FIG. 5. Megaspores with attached microspores of *Selaginella selaginoides* (A) and *S. helvetica* (B): Scale bars 100 μm.

distances, this study also shows that substantial heights above the plants are reached during spore ejection, which in *S. selaginoides* was up to 76 cm at 3 cm distance from the shoots.

The observed active ejection of megaspores was obtained under artificial laboratory conditions, but still reflects the power of the megasporangia in dispersing the megaspores. With the slingshot mechanism, dispersal does not only happen horizontally, but also vertically, and we recorded a maximum height of 85 cm in *Selaginella selaginoides*. The outdoor-experiment revealed much larger dispersal distances due to wind assistance. Under these conditions, both mega- and microspores showed a leptokurtic dispersal distribution, which is comparable to results in mosses and of pollen in flowering plants (Miles and Longton, 1992; Ghazoul, 2005; Friedman and Barrett, 2006). Crucially, the dispersal distances of mega- and microspores overlapped considerably, allowing for self- fertilization as shown, *e.g.,* in *S. apoda* (Schulz *et al.,* 2010). Furthermore, we observed electrostatic adherence of microspores to the megaspores, which may even take place before active dispersal, also resulting in joint dispersal and potentially in self-fertilization. This synaptospory (Kramer, 1977; Wang, Zhang, and Liu, 2018) may be an important mechanism to ensure fertilization.

Our results also indicate that there are differences in these active dispersal distances between species of *Selaginella*. These may be related to the different environmental conditions under which the species grow, but more species would have to be studied also in the tropical environment before firm conclusions can be drawn.

While our experiments do not provide direct observations on the poorly known mating system in *Selaginella* (Sessa, Testo, and Watkins, 2016), it seems unlikely that self-incompatibility occurs. Since under natural conditions microspores are likely to be transported over much larger distances than observed in our experiments, outcrossing would be possible when reaching megaspore dispersal areas of plants in the neighborhood. Indeed, the results of VanBuren *et al.* (2018) reveal high heterozygosity in members of the genus which is presumably a result of outcrossing.

In conclusion, the evolution of heterospory in *Selaginella*, with many small male spores and a smaller number of large female spores (Petersen and Burd, 2016, 2018b), posed the species of *Selaginella* with the challenge of ensuring that after dispersal micro- and macrospores would be in close enough proximity to allow successful fertilization. As shown in here and in previous studies, this is achieved by active spore ejection of the megaspores and electrostatic adherence of the microspores to the megaspores. By overcoming these challenges, *Selaginella* was able to take advantage of the evolutionary innovations of heterospory and of producing both self-fertilized and outcrossed offspring (Petersen and Burd 2016).

Acknowledgements

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SHORTER NOTES

Pteris tremula **(Polypodiopsida: Pteridaceae): A Naturalized Species in Argentina.**—The cosmopolitan fern genus *Pteris* L. (subfamily Pteridoideae, Pteridaceae; PPG I, Journal of Systematics and Evolution 54:563–603. 2016), is one of the most diverse, including approximately 250 species that inhabit temperate, tropical, and subtropical regions of all continents from Australia, New Zealand, South Africa, and South America northward to Japan and North America. The species grow from open slopes to dense forests and from acid soils to limestone rock; about 60 taxa occur in the tropical Americas (Liao, Ding, Wu, Prado, and Gilbert, Flora of China 2–3:181–211. 2013., Chao, Rouhan, Amoroso, and Chiou, Annals of Botany 114:109–124. 2014). Some species, such as *Pteris cretica* L.*, P. longifolia* L., *P. multifida* Poir.*, P. tremula* R. Br., and *P. vittata* L. are reported as invasive plants in many parts of the world, being increasingly found in both, natural and urban areas in several countries possibly as a result of climate change and human migration. Some grow so prolifically that they have been classified as invasive weeds (Wilkins and Salter, Bulletin of the Royal Society of Chemistry:8–10. 2003, Robinson, Sheffield, and Sharpe, In Mehltreter, Walker, and Sharpe, Fern Ecology:255–322. 2010). Among them, *Pteris cretica, P. multifida* and *P. vittata* are species that originated in Asia (China) or Europe and have been cited as naturalized in many regions of America since the early 1970s (*e.g.,* de la Sota, Colección Científica del Instituto Nacional de Tecnología Agropecuaria 13:1–275. 1977; Prado and Windisch, Boletim do Instituto de Botânica São Paulo 13:103–199. 2000; Mazumdar and Arana, Phytotaxa 261:199–200. 2016). *Pteris tremula* belongs to the *Pteris chilensis* clade, characterized by three to four-pinnatifid lamina, ultimate pinnules (lobes) with veins free (Zhang, Rothfels, Ebihara, Schuettpelz, Le Péchon, Kamau, He, Zhou, Prado, Field, Yatskievych, Gao, and Zhang, Cladistics 31:1–18. 2014). The clade contains only two species with disjunct distributions, the Chilean endemic *Pteris chilensis* Desv. and *Pteris tremula*, known as "tender brakefern" and originally distributed in the Australasian South Pacific, in Australia and Norfolk Island, Lord Howe Island, New Zealand, Kermadec Island, and Fiji (Kramer and Mc Carthy, Flora of Australia 48:242–248. 1998), often locally naturalized in the Northern Hemisphere (Zhang *et al.*, 2014). Also, *P. tremula* has been cited as an invasive weed in South Africa (Baard and Kraaij, South African Journal of Botany 94:51–63. 2014).

In the last 10 years, the Argentinian flora has been continuously enriched with new alien plant species, which represents a serious problem particularly in the natural environments that are threatened by habitat loss and fragmentation (Hoyos, Gavier-Pizarro, Kuemmerle, Bucher, Radeloff, and Tecco, Biological Invasions 12:3261–3275. 2010; Oggero and Arana, Hoehnea 39:169–197. 2012). Human alterations of natural environments are probably irreversibly changing these systems into novel ecosystems through severe modifications both in the abiotic conditions and the biotic composition (Hobbs, Higgs, and Harris, Trends in Ecology and Evolution 24:599–605. 2009). The presence of exotic species in an ecosystem can produce not only profound changes in community structure, but also in ecosystem functioning (Godoy, Castro-Díez, van Logtestijn, Cornelissen, and Valladares, Oecologia 162:781–790. 2010). Some of these alien species can become invasive, threatening natural and agricultural ecosystems, causing damage to the economy and human health (Gavier-Pizarro, Radeloff, Stewart, Huebner, and Keuler, Ecological Applications 20:1913–1925. 2010).

As part of the projects that investigate the diversity of ferns in Argentina (www.floraargentina.edu.ar) and their conservation status, at least five populations of *Pteris tremula* were registered growing naturally in the Argentinian coast of Río de la Plata. To consider this taxon as naturalized, we followed the criteria provided by Richardson *et al.* (Richardson, Pyšek, Rejmánek, Barbour, Panetta, and West, Diversity and Distribution 6:93-107. 2000) and Pyšek *et al.* (Pyšek, Richardson, Rejmanek, Webster, Williamson, and Kirschner, Taxon 53:131-143. 2004), which define naturalized plants as “Alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade natural, seminatural, or human-made ecosystems”. At least three populations of *Pteris tremula* grow in Punta Lara Natural Reserve, Mirador del Sendero Chiricote, 6-XII-2006, *Giudice et al. 25* (LP); Sendero del Che (34°47′24.58″ S 58°1′29.17″ W), 24-V-2015, *Berrueta et al. 95* (LP, RCVC); Canal Baldovinos (34°45′58.74″ S 58°5′2.95″ W), 3-VI-2018, *Berrueta & Gorrer 15* (LP, RCVC). Another population occurs a little further north, at Pdo. Avellaneda, Sarandí, calle Nicaragua y Acceso Sudeste, Eco Área Reserva Ecológica Municipal de Avellaneda (34°65′47.56″ S 58°31′67.72″W), *Berrueta s/n°* (LP) and many specimens were found growing as epiphytes on *Melia azedarach* L. (Meliaceae) trees near San Isidro, Buenos Aires. It is interesting to mention that, in order to estimate how long the species has been colonizing the natural environments in Argentina, the first recorded specimen of *P. tremula* was collected in the field in Tigre, Buenos Aires, XII-1905, by *L. Haumann* (SI 24585). Years later, many specimens were registered as “sub spontaneous in wet places, reproducing by spores from dried fronds” (handwritten label information) in the Belgrano neighbourhood, city of Buenos Aires, 5-III-1932, *A. Burkart 5680* (SI). Biogeographically, all the mentioned areas are included in the Chaco Domain, Eastern Pampean District of the Pampean Province (Arana, Martinez, Oggero, Natale, and Morrone, Zootaxa 4341:420–422. 2017). In this zone, proximity to the la Plata river determines a great variety of ecological niches. There are savannas, with species of Poaceae (that can reach 1 m in height), herbs, and shrubs. There are also seasonally dry tropical forests similar to those of the Chaco province; flooded savannas; and gallery forests along the rivers. The particular floristic association of the forests comprises tree species such as *Blepharocalyx salicifolius* (Kunth) O. Berg (Myrtaceae), *Allophylus edulis* (A. St.-Hil., A.

Juss. & Cambess.) Hieron. ex Niederl. (Sapindaceae), *Ocotea acutifolia* (Nees) Mez (Lauraceae), *Pouteria salicifolia* (Spreng.) Radlk. (Sapotaceae) and *Lonchocarpus nitidus* (Vogel) Benth. (Fabaceae). In such habitats, ferns grow mainly associated with the gallery forests that border the internal streams, locally called marginal forests (Giudice, Ramos Giacosa, Luna, Yañez, and de la Sota, Revista de Biología Tropical 59:1037-1046. 2011). Periodic observations from 2006 to the present allowed us to observe that *P. tremula* colonized new places, both natural (in reserves) and disturbed places, thus expanding its distribution and number of individuals (Fig. 1 A-F). Sporophytes of different sizes (therefore attributable to different ages) were registered (Fig. 1 D-E). Reporting those newly alien species in Argentinian flora, and monitoring the spread of those previously reported, can be useful tools in establishing measures to eradicate them before they become invasive and harmful, especially in protected areas. We thank the staff of Punta Lara Natural Reserve for their help during field trips. This study was supported by Research Projects of Universidad Nacional de La Plata, Argentina (11/N725 and 11/N850).—MARCELO DANIEL ARANA, Plantas vasculares, Departamento de Ciencias Naturales, Facultad de Ciencias Exactas, Físico-Químicas y Naturales, ICBIA (UNRC-CONICET), Universidad Nacional de Río Cuarto, Ruta 36 km 601, X5804ZAB Río Cuarto, Córdoba, Argentina, PEDRO C. BERRUETA, DANIEL GORRER, GABRIELA ELENA GIUDICE AND MARÍA LUJÁN LUNA, Laboratorio de Anatomía comparada, Propagación y Conservación de Embriofitas "Dr Elías de la Sota", Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Boulevard 120 entre 61 y 64, B1900FWA La Plata, CONICET, CIC-BA, Buenos Aires, Argentina.

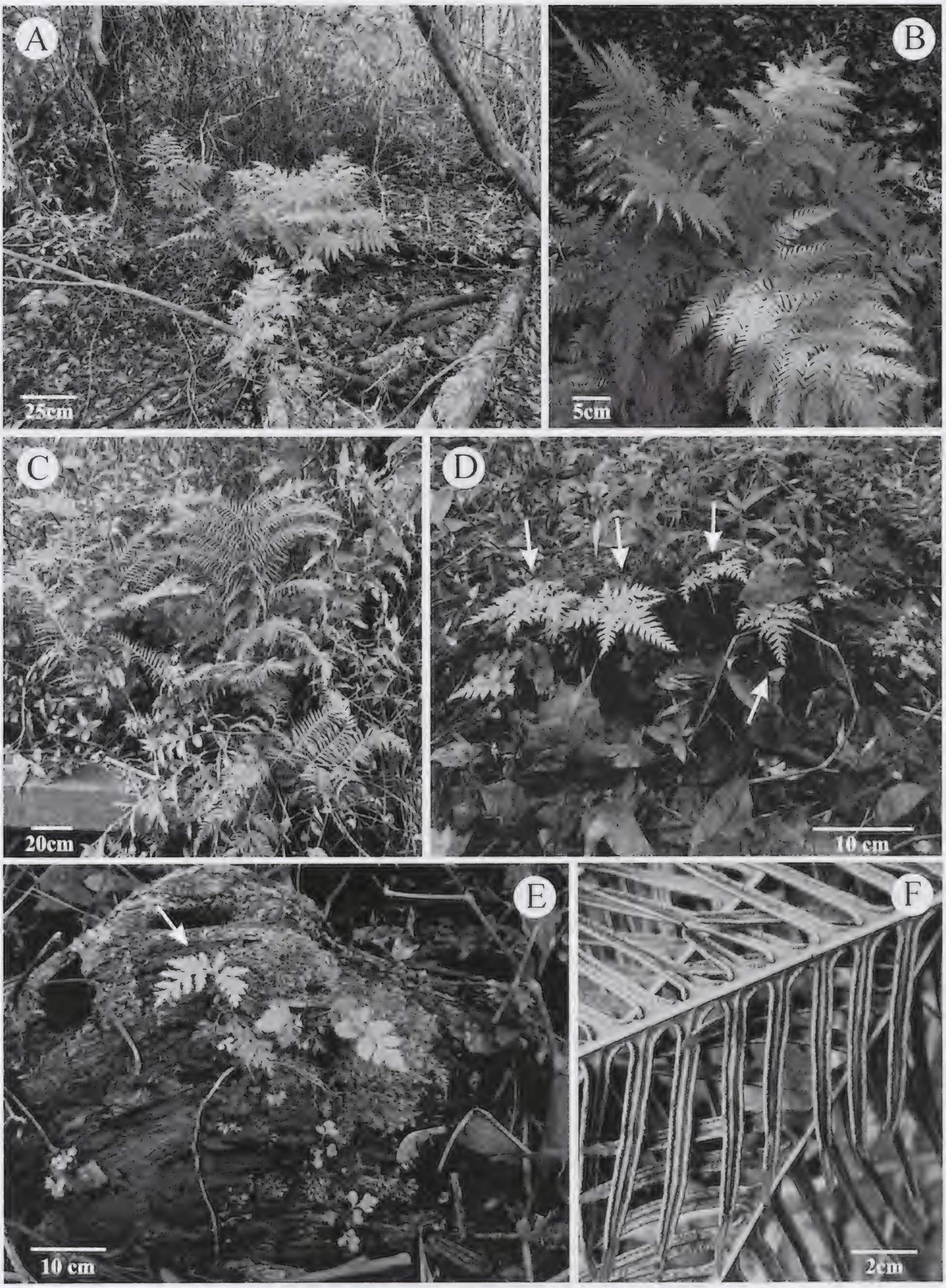

FIG. 1. *Pteris tremula* populations in the Punta Lara Natural Reserve. A. Population established in "Sendero del Che". B. Details of the leaves. C. Population of "Mirador del Sendero Chiricote". D. Young individuals growing among the leaf litter (arrows). E. Young sporophyte growing on a fallen tree trunk (arrow). F. Fertile pinna.

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SHORTER NOTES

First Evidence of Naturalization of the Black Tree Fern, *Cyathea medullaris*, in Madeira Island (Portugal).—Widely known as the black tree fern, *Cyathea medullaris* (G. Forst.) Sw. is a large fern of the family Cyatheaceae attaining 20 m in height (Large and Braggins, *Tree Ferns*. Timber Press, Inc. 2004). It is distributed along several archipelagos of the south-west Pacific Ocean: Fiji, Marquesas, Tahiti, Austral Islands, Pitcairn, and New Zealand (Large and Braggins, 2004). Its occurrence in areas whose climates range from equatorial to temperate maritime corresponds to a high degree of ecological amplitude of this fern species. In New Zealand, where the black tree fern is widely distributed, it is common in the lowland forests of the North island, but more localised in the South Island, being less common in drier eastern ecosystems. Within its distribution in New Zealand, the zones experiencing coldest winters are sited along western and southern South Island and in Stewart Island (Brock, The influence of tree ferns on the composition and structure of New Zealand native forests. The University of Auckland. 2017). According to the USDA Hardiness Zone Classification, these regions fall within zone 9b, which is characterized by an average annual minimum temperature between -6.7 and -3.9°C (Sturman, *The Weather and Climate of Australia and New Zealand*. Oxford University Press. 1996). This tree fern species is fast-growing and regarded as the most adaptable member of the genus in New Zealand, where it is found growing in a wide range of habitats: unlike the other *Cyathea* species, it typically colonizes open places with full exposure to sun and wind (Brock, 2017). Recent research has shown evidence of its importance as a pioneer plant colonizing disturbed areas and edge environments (Brock, Perry, Lee, Schwendenmann, and Burns, New Zealand Journal of Ecology 42:18-30. 2018).

A small, healthy population of *Cyathea medullaris*, possibly recently introduced was found during a week spent on the Portuguese island of Madeira in July 2016. The site in which the alien tree fern species had been introduced is on a mountain slope in the North West part of Madeira island close to Ribeira da Janela (Porto Moniz Municipality). The area, whose geological substrate consists in Miocene/Pliocene pyroclastics and lavas, has a north-east orientation and lies at an altitude of about 500 meters above sea level (USDA Hardiness Zone 11a). A voucher specimen labelled GE1421 has been deposited in the Herbarium Universitatis Genuensis (GE). It was identified using the key to genus *Cyathea* included in Brownsey and Perrie. Cyatheaceae. *In*: Breitwieser, Heenan, and Wilton (eds.). *Flora of New Zealand – Ferns and Lycophytes*. Fascicle 13. Manaaki Whenua Press. 2015.

In Table 1 are summarized the main characters differentiating *Cyathea medullaris* from the other tree fern species naturalized in Madeira: *Cyathea cooperi* (Haook. ex F. Muell.) Domin and *Dicksonia antarctica* Labill. The morphology of stipe scales was an important diagnostic feature to differentiate

TABLE 1. Main characters differentiating the three tree fern species naturalized in Madeira (data gathered from: Large and Braggins, 2004; Brownsey and Perrie, 2015).

Characters	***Cyathea medullaris***	***Cyathea cooperi***	***Dicksonia antarctica***
Trunk diameter	20 cm	15 cm	2 m
Trunk height	20 m	10-12 m	6 m
Scars left by fallen fronds	Hexagonal	Oval	Absent
Fronds	Tripinnate; length 6 m	Bi- or tripinnate; length 4-5 m	Tripinnate; length 4.5 m
Rachis and stipe coloration	Black	Greenish to brown	Rachis greenish to brown, stipe brown
Stipe scales	Blackish or dark brown with dark-colored setae on margins	Two types: one dark red or brown with red setae on margins; the other large and papery-white with red setae on margins	No scales, but bristly hairs which are shed after uncoiling
Sori	In pairs of two to six	Singly or in rows of as many as ten	Two to six per pinnule lobe
Indusia	Present	Absent	Present

Cyathea medullaris and *Cyathea cooperi*, especially among young plants that had not yet developed sporangia (Fig.1).

The largest individuals of *Cyathea medullaris* observed were three impressive plants that had been planted along the left side of a ramp leading to the entrance to a private estate (32°50′29,62″N; 17°9′10,02″W), along road ER209 connecting Ribeira da Janela to Madalena do Mar. Presumably they had not been planted before 2010, based on a picture of this area, dated November 2009, in Google Maps: at that time the villa and the fence were not there, and neither were the tree ferns. These individuals, which showed a basal diameter around 20 cm and a trunk height between 1.5 and 2 m (Fig. 2), appeared very vigorous, and had huge fronds covered with fertile sporangia.

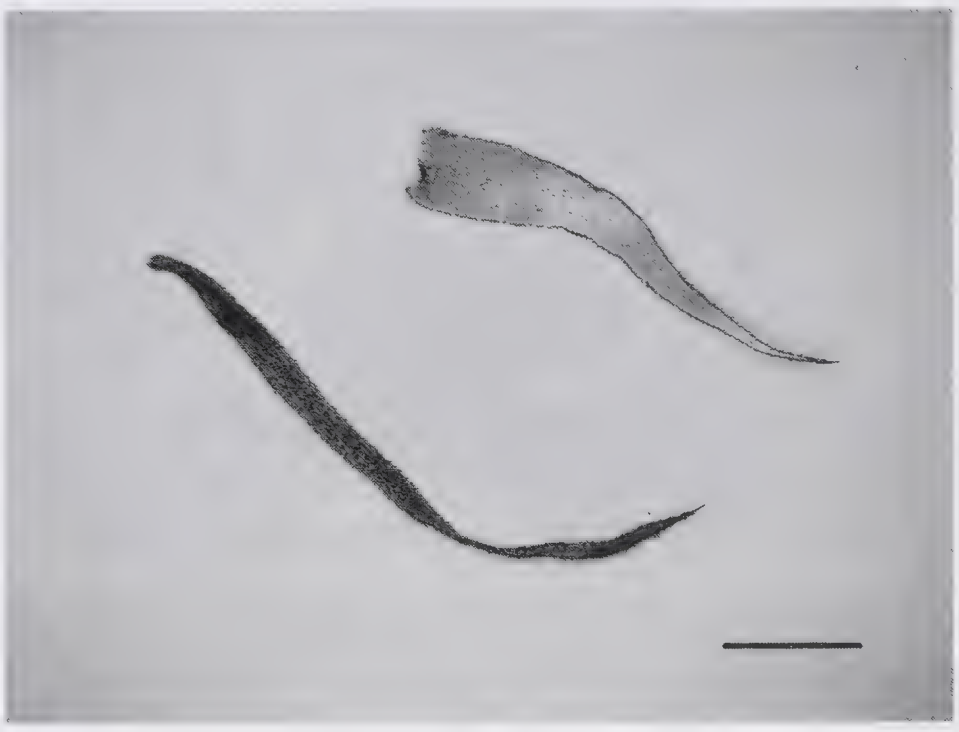

FIG. 1. Comparison between stipe scales of *Cyathea medullaris* (bottom) and *Cyathea cooperi* (top). Scale bar = 5 mm.

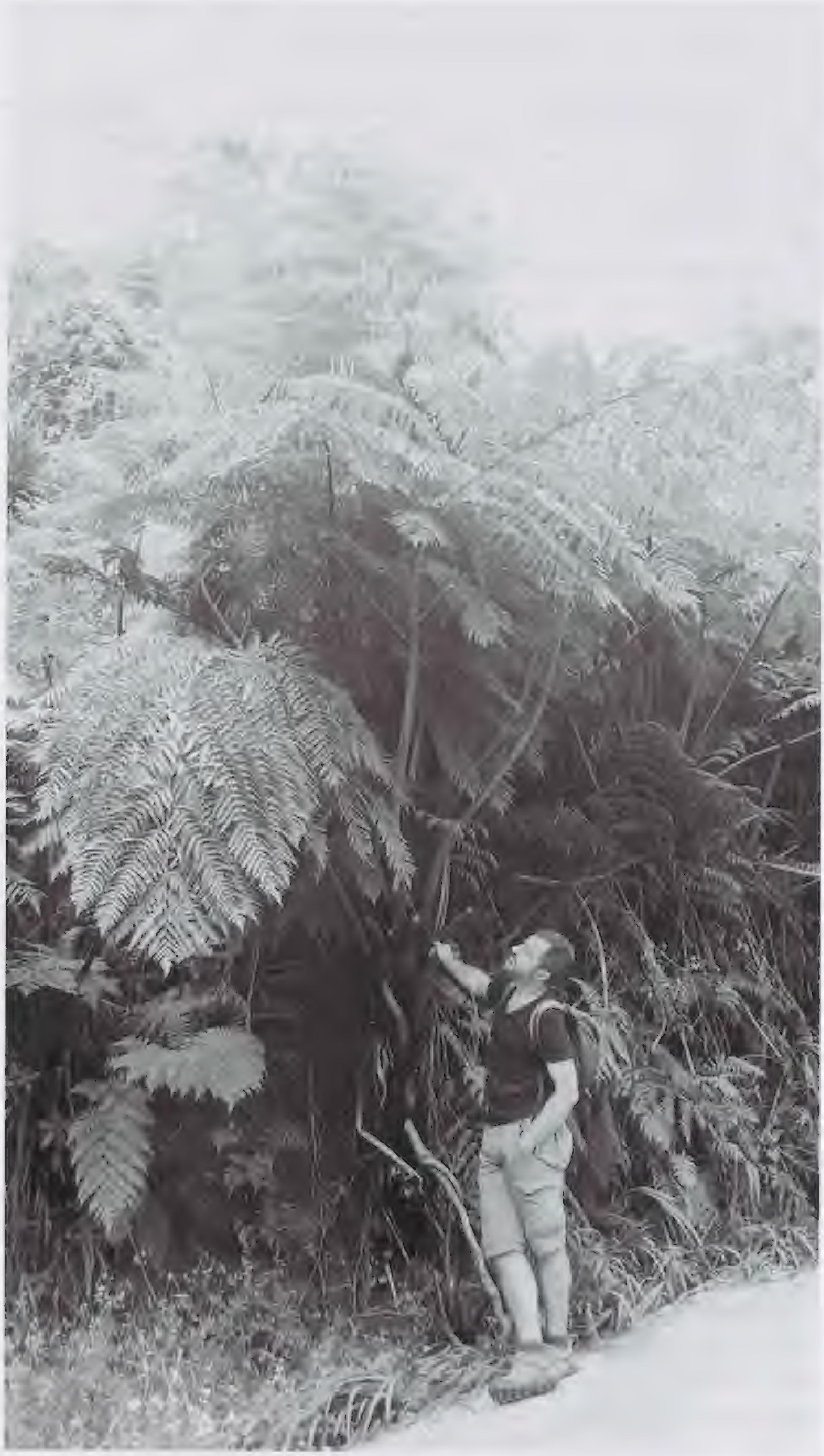

FIG. 2. One of the impressive specimens of *Cyathea medullaris* planted along the ramp cited in the text (NW Madeira Island, Portugal).

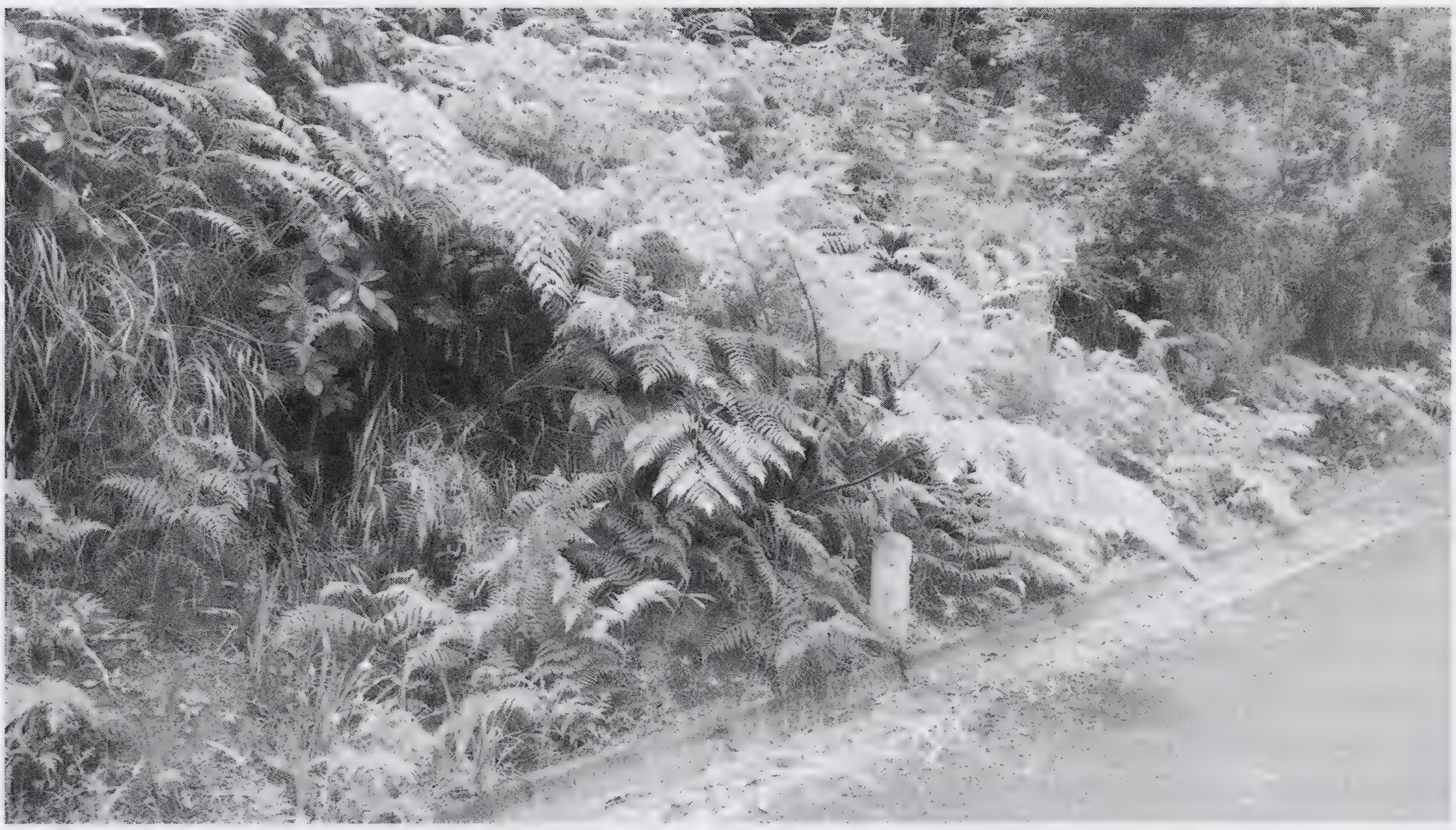

FIG. 3. Young plants of *Cyathea medullaris* growing along road ER209 (NW Madeira Island, Portugal).

A large number of younger plants of the same species could be observed under the three tree ferns, inside the narrow drainage ditch separating the estate garden from the adjacent tree plantation and along a stretch of road ER209 starting about 600 m uphill of the property and ending 50 m downhill (Fig. 3); their size ranged from sporelings with 20-25 cm fronds to plants showing 60-70 cm tall trunks. All the young black tree ferns examined by us had not yet developed sporangia. Along the road, the juvenile tree ferns were rather sparse, but within the drainage ditch they reached high densities, which caused the common occurrence of coalesced plants.

The main vegetation type of the area is a tree plantation dominated by tall non-native trees, such as *Pinus pinaster* Aiton and *Eucalyptus globulus* Labill., with a prevalence of native ferns, such as *Diplazium caudatum* (Cav.) Jermy and *Woodwardia radicans* (L.) Sm. as the undergrowth. Interestingly, no black tree fern plants were observed inside the tree plantation undergrowth, possibly because they were outcompeted.

It must be emphasized that this is not the first record of the naturalization of *Cyathea medullaris* in the Macaronesian islands, since this tree fern species, together with *Cyathea cooperi*, has been already reported for São Miguel in the Azores Archipelago (Brownsey and Perrie, 2015; Costa, Foody, Jiménez, and Silva. ISPRS International Journal of Geo-Information 4: 2496-2518. 2015). Even if data on the invasiveness of *Cyathea medullaris* in São Miguel are lacking, its potential role as an invasive plant in Madeira island should not be underestimated. The rapid spread of this tree fern species over a short timespan clearly shows that it has found suitable microclimatic and ecological conditions. In addition, this species has a huge spore production, estimated at

2 kg of spores per individual per year (Large and Braggins, 2004). This adaptative character and abundant reproduction and dispersal by spores may lead, in the near future, to the impossibility of controling its spread across Madeira Island, within the habitats suitable for it. It would be a "déjà vu", considering what has occurred with the congeneric Australian lacy tree fern *Cyathea cooperi*, which was imported into Madeira for ornamental purposes since before 1934 (Vieira, *Flora da Madeira: Plantas Vasculares Naturalizadas no Arquipelago da Madeira*. Museu Municipal do Funchal. 2002) and planted widely, even along nature trails in laurisilva (native laurel forest) (pers. obs.). This species, which is well known worldwide for its high degree of invasiveness (Palmer, *Hawai'i's Ferns and Fern Allies*. University of Hawai'i Press. 1995), has spread across Madeira island, especially within the humid ecosystems. In several parts of the laurel forest, which is the largest patch of Macaronesian laurisilva and has been declared a World Heritage Site by UNESCO for its unique biodiversity, the lacy tree fern has become a common fern species rising above the native ferns, for instance in the Municipalities of Ribeira da Janela, Funduras, and Lombo do Meio (Vieira, 2002). According to this author, 11 non-native fern and lycophyte taxa belonging to eight families (Adiantaceae, Blechnaceae, Cyatheaceae, Davalliaceae, Dicksoniaceae, Dryopteridaceae, Pteridaceae, and Selaginellaceae) have established self-sustaining populations in Madeira: 8 of these taxa have been reported in the laurisilva or in proximity to it. These latter ones include the soft tree fern, *Dicksonia antarctica*, cultivated in Madeira since at least 1942 and recorded for the first time in Madeiran laurisilva in 1978 (Vieira, 2002). In the same publication it is noted that, compared to *Cyathea cooperi*, *Dicksonia antarctica* occurs in Madeira with lower diffusion and density. In São Miguel in the Azores Archipelago, where it was probably introduced in the nineteenth century, the soft tree fern has spread to a mountain area of over 48 km^2 threatening two habitats of European conservation priority: laurisilva forests and blanket bogs (Arosa, Ceia, Quintanilla, and Ramos. Biological Invasions 14:1317-1323. 2012).

The authors are very grateful to Prof. Francesco Orsino, formerly Professor of Botany and Plant Ecology at Genoa University, who made valuable comments on a draft of this manuscript. Our thanks are due also to Prof. Pina Barberis (Professor of Botany at Genoa University) and Dr. Davide Dagnino (Herbarium Universitatis Genuensis).—RICCARDO JESU[1] AND RICCARDO ANFONSO[2]. [1]ITTL "Nautico San Giorgio", Edificio Calata Darsena, Postal Code: 16126, Genova, Italy, email: riccardojesu@libero.it. [2]Gruppo SIGLA srl c/o Costa Crociere SpA, Piazza Piccapietra 48, Postal Code: 16121, Genova, Italy, email: r.anfonso@libero.it.

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SHORTER NOTES

Goniopteris moranii **(syn.:** ***Thelypteris guadalupensis*****; Thelypteridaceae), New to Florida and the Continental United States.**—While conducting rare plant surveys in southeast Florida (Broward County) we encountered a population of a fern that was recognized by the primary author as a species not currently known as part of the flora of Florida (Wunderlin, Hansen, Franck, and Essig, Atlas of Florida Plants. 2019). We collected a specimen and took photographs (Fig. 1A-D). We shared images with *Thelypteris* expert Susan Fawcett (University of Vermont) who confirmed the identity of the species as *Goniopteris moranii* C. Sánchez, or, if *Thelypteris* is treated in its broadest sense, *Thelypteris guadalupensis* (Wikstr.) Proctor.

The family Thelypteridaceae is known to be taxonomically rich, comprising circa 950 species (Smith, Pryer, Schuettpelz, Korall, Schneider, and Wolf, Taxon 55:705–731. 2006) with significant contributions to fern diversity in the tropics and subtropics (Smith, Pteridophyta of Peru. 1–80. 1992), although the generic resolution of the family remains complex (Almeida, Elias, Hennequin, Schneider, Smith, Batista, Ramalho, Proite, and Salino, Molecular Phylogenetics and Evolution 94:688–700. 2016). Recent taxonomies have elevated *Thelypteris* subgenus *Goniopteris* to genus *Goniopteris* (Almeida, Elias, Hennequin, Schneider, Smith, Batista, Ramalho, Proite, and Salino, 2016; Pteridophyte Phylogeny Group I. Journal of Systematics and Evolution 54:563–603. 2016). Our specimen matches the description of *Goniopteris moranii* C. Sánchez (Sánchez, Brittonia. ISSN:1938–436X(electronic). 2017). *Goniopteris moranii* is a widespread species occurring throughout the Greater and Lesser Antilles as well as southeastern Mexico (Quintana Roo) (Riba and Torres, American Fern Journal 83:39. 1993). *Goniopteris moranii* is the fourth member of *Goniopteris* to be documented from Florida, and the third from South Florida. The other species include: *G. tetragona* (Sw.) C. Presl, known from five counties in Central Florida, *G. reptans* (J.F.Gmel.) C. Presl, recorded from nine counties in both South and Central Florida, and the state-endangered, *G. sclerophylla* (Poepp. ex Spreng.) Wherry, known only from Miami-Dade County in South Florida (Wunderlin, *et al.*, 2019). *Goniopteris moranii* is distinguished from these species by each mature frond being mostly simple-pinnatifid with only 1-4 pairs of free pinnae near the base.

The area where the plants were found was an outcrop of shallow karst topography within a larger matrix of pond cypress (*Taxodium ascendens* Brongn.), laurel oak (*Quercus laurifolia* Michx.), and red maple (*Acer rubrum* L.) swamp adjacent to mixed pine/palmetto uplands with a tropical hardwood component. The canopy was variable but low (< 2 m), and dense, dominated primarily by one very large *Schinus terebinthifolia* Raddi, with abundant *Schefflera actinophylla* (Endl.) Harms and *Ardisia elliptica* Thunb., and scattered *Bischofia javanica* Blume., *Ardisia escallanioides* Schltdl. & Cham., *Eugenia axillaris* (Sw.) Willd., and *Psychotria nervosa* Sw. Other ferns

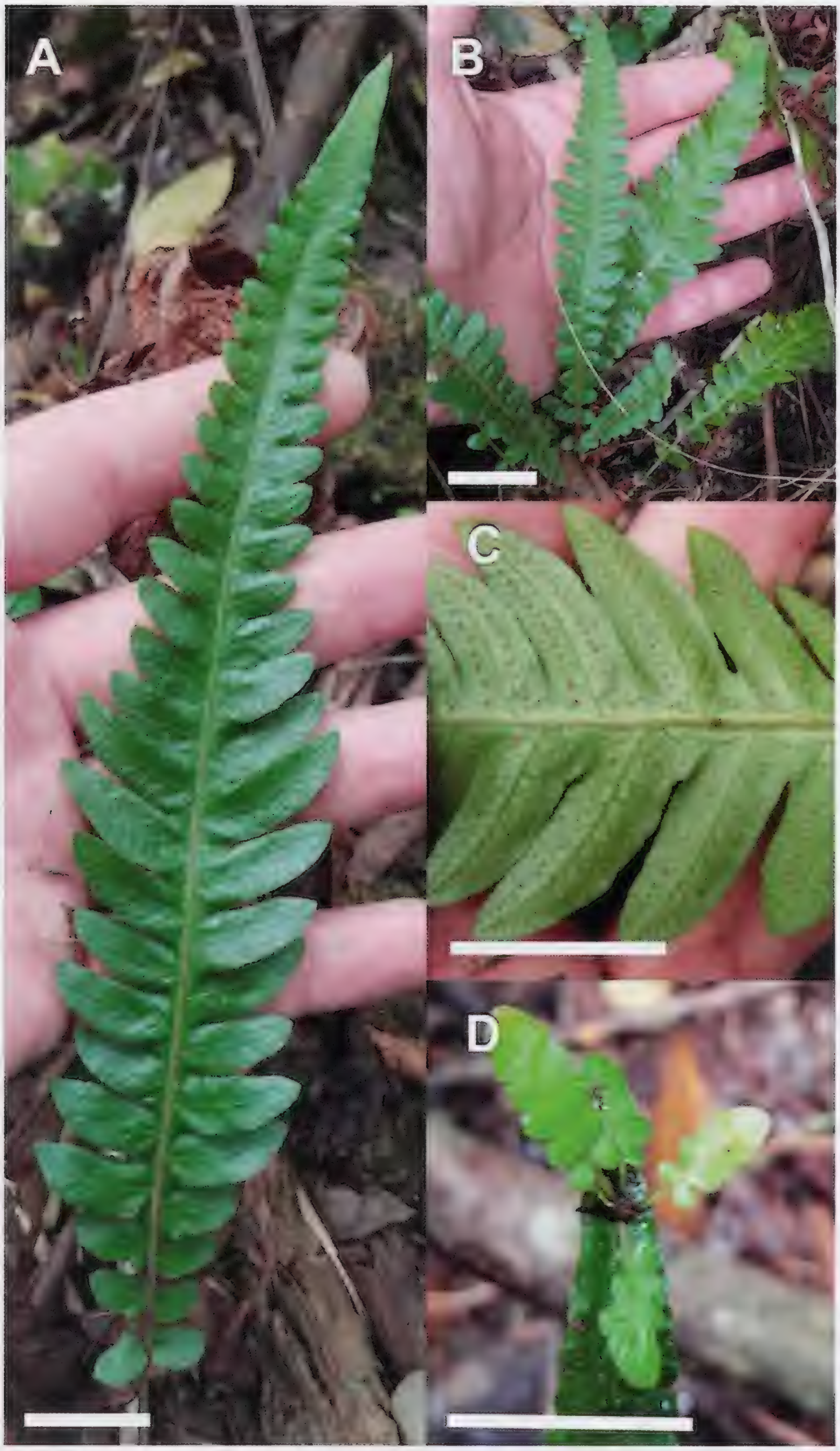

FIG. 1 A. Habit of mature *Goniopteris moranii* frond. B. Fronds of immature sporophyte. C. Sporangia on the abaxial surface of *G. moranii* frond. D. A single proliferous bud with plantlet at apex of frond. Bars = 2 cm.

present— in order of abundance— were: the invasive *Tectaria incisa* Cav., *Nephrolepis exaltata* (L.) Schott, *Thelypteris kunthii* (Desv.) C. V. Morton, and the state-endangered *Ctenitis sloanei* (Poepp. ex Spreng.) C. V. Morton. A total of 35 reproductive-sized plants (Fig. 1A) and 283 identifiable, immature sporophytes (Fig. 1B) were observed for a total of 318 individuals over approximately 100 m^2. All reproductive-sized individuals were growing in soil surrounding shallow solution holes, whereas most smaller individuals were on bare rock or nearly so. Sporangia were observed and photographed on one specimen (Fig. 1C). The species also produces proliferous buds toward the apex of the frond (Fig. 1D).

There are several similar species in the Caribbean that could potentially be confused with *G. moranii* worth mentioning due to their geographic proximity. *Goniopteris scolopendrioides* (L.) C. Presl is pinnatifid throughout, while *G. moranii* possesses 1-4 pairs of free pinnae on mature fronds. The Cuban endemic, *G. jarucoensis* (Caluff & C. Sánchez) Salino & T. E. Almeida has 9-15 pairs of free pinnae. The morphologically similar *G. hildae* (Proctor) Salino & T. E. Almeida is most easily distinguished by habitat, growing exclusively "in crevices of [limestone] ledges and cliffs" while *G. moranii* is recognized as growing nearly always terrestrial in soil, limestone or calcareous substrate, or sometimes on mossy stones, comparable to this discovery in Florida (Proctor, American Fern Journal 75:56–70. 1985; Proctor, Memoirs of the New York Botanical Garden, 53:1–389. 1989). *Goniopteris moranii* is reported to hybridize with *G. hastata* Fee, *G. hildae,* and *G. reptans* (Proctor, 1989). Of these, only *G. reptans* is known from South Florida and in fact co-occurs at the site where *G. moranii* was discovered, though populations are separated by over 700 m and no hybrids have been observed.

Goniopteris species are uncommon in cultivation, and an online search for *G. moranii* and synonyms being cultivated or for sale yielded no results. This included Botanic Gardens Conservation International (BGCI.org), where there are no records of ex situ collections of this species worldwide. The species is not particularly showy and likely has little to no ornamental value outside the community of fern enthusiasts. The species appears restricted to areas of karst topography and appears to be rather slow growing. These factors combine to make anthropogenic introduction unlikely, despite the suite of non-native species at the site. Although it seems unlikely that the species was directly introduced by humans to this location, the timing of its arrival to Florida is uncertain. The site is a Broward County nature center with high conservation value and thus has been heavily botanized in the past by Dan Austin, Patricia Howell, and others. This perhaps would imply a recent arrival by spore from the closest populations in central or western Cuba, circa 400 – 500 km from our site (Sánchez, 2017), but it is also plausible that the population has been resident in Florida for a longer period of time.

Voucher: **Florida.** Broward County: Coconut Creek. Fern Forest Nature Center. Colony of ~200 sporophytes- several dozen of reproductive size found on edges of solution holes beneath dense canopy of *Schinus terebinthifolia* with scattered *Schefflera actinophylla. Tectaria incisa, Nephrolepis exaltata,* and *Ctenitis sloanei* in the immediate area. Proliferous bud observed on single frond, removed for conservation propagation. Very short, creeping rhizome. Removed only a portion of mature plant. New record for continental U.S. 27 December 2018, *Lange* 78 (FTBG) and August 2019, *Lange* 140 (University of South Florida).

KEY TO FLORIDA *GONIOPTERIS*

1. Leaf blade 15-25 cm wide, abruptly narrowed to the apex, the apical pinna similar to the lateral pinnae but appearing stalked .... ***G. tetragona***
1. Leaf blade to 10 cm wide, gradually narrowed to the apex, the apical pinna pinnatifid and not similar to the lateral pinnae.
    2. Pinnae with pointed teeth throughout; blades monomorphic and erect, not rooting at the apex .... ***G. sclerophylla***
    2. Pinnae entire, crenulate, or lobed but not as above; blades somewhat dimorphic, the sterile ones shorter and spreading or prostrate, the mature fronds erect, ascending, or spreading, sometimes rooting at the apex.
        3. Mature leaf blades spreading to ascending; terminal pinna simple-pinnatifid, but this <1/2 the length of the blade .... ***G. reptans***
        3. Mature leaf blades erect; simple-pinnatifid for > 3/4 the length (with 1-4 free pairs of basal pinnae) .... ***G. moranii***

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COVER CAPTION: Fertile pinnae of *Anemia tabascana*. Photo credit: C. I. Carvajal-Hernández.